

## Phylogenetic analysis and preliminary classification of the Parathalassiinae (Diptera: Empidoidea: Dolichopodidae *sensu lato*)

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### Abstract

Phylogenetic relationships of the subgroups of Parathalassiinae are presented, based on a morphological cladistic analysis. Worldwide, all known extant genera, species groups and newly discovered undescribed lineages are represented in the analysis. Some previously proposed generic relationships are supported by the analysis, but recognition of many current genera renders the present concept of *Microphorella* Becker as both paraphyletic and polyphyletic. *Microphorella merzi* Gatt is here classified in *Eothalassius* Shamshev & Grootaert, as *Eothalassius merzi* (Gatt) **comb. nov.** A preliminary classification with all included extant lineages within the Parathalassiinae (at the genus and species group level) is outlined. The ranking of these lineages is discussed and several species groups of *Microphorella* may need to be elevated to generic or subgeneric level, whereas some currently recognized genera may need to be relegated to subgenera.

**Key words:** Classification, morphology, phylogeny, genera, subgenera, species groups, *Microphorella*, Empidoidea, Dolichopodidae, Parathalassiinae

### Introduction

The empidoid subfamily Parathalassiinae is one of the basal lineages of the Dolichopodidae *s.lat.*, along with the Microphorinae (Sinclair & Cumming 2006). Members of the Parathalassiinae are small (1.0–3.9 mm), rarely collected flies, that generally inhabit rocky or sandy sea coasts, river banks and stream margins (Figs 1–11). At present, nothing is known of the immature stages or the habitats they occupy, but larval parathalassiines are probably predaceous and live in sandy, stony or muddy riparian and coastal shorelines.

World-wide the subfamily currently includes 51 described extant species in eight genera (Brooks & Cumming 2016, 2017, 2018). These genera were described as follows: *Parathalassius* Mik (1891), *Microphorella* Becker (1909), *Thalassophorus* Saigusa (1986), *Plesiothalassius* Ulrich (1991), *Amphithalassius* Ulrich (1991), *Chimerothalassius* Shamshev & Grootaert (2002), *Eothalassius* Shamshev & Grootaert (2005), and *Neothalassius* Brooks & Cumming (2016). In addition, there are three fossil genera, namely *Archichrysotus* Negrobov (1978), *Cretomicrophorus* Negrobov (1978) and *Retinitus* Negrobov (1978) known from various Late Cretaceous ambers (Grimaldi & Cumming 1999), and *Electrophorella* Cumming & Brooks (2002) known from Baltic amber. Described species diversity in each extant genus is indicated under “Preliminary classification of the Parathalassiinae” (see below) along with the number of undescribed species presently known in each group (*i.e.*, 45 additional undescribed species in total).

Although Cumming & Brooks (2002, 2006, 2018) and Brooks & Cumming (2010) have discussed relationships within the Parathalassiinae at the generic level, no thorough phylogeny has been published. The present generic concepts have not been rigorously analyzed and at least *Microphorella* as currently recognized, appears both paraphyletic and polyphyletic. Since adult parathalassiines are generally rarely collected and uncommon in collections, a meaningful analysis of molecular sequence data from representatives of all known lineages is not possible at this time. The purpose of this paper is to cladistically analyze morphological characters of all known extant genera, species groups and recently discovered undescribed lineages in the Parathalassiinae. Based on this analysis, a preliminary classification of the subfamily is provided as a framework for future revisionary work.



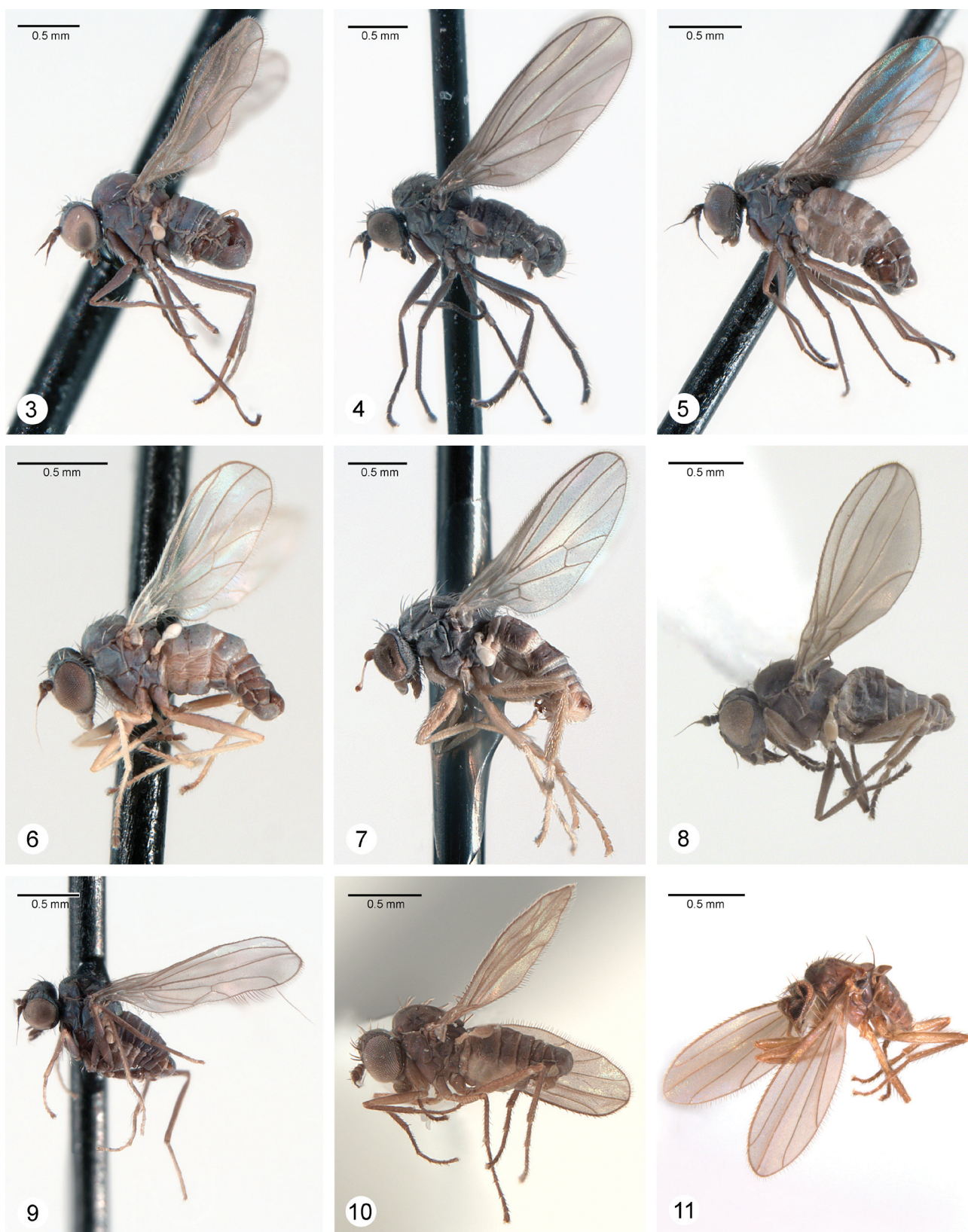
**FIGURES 1–2.** Habitus photographs of live specimens of Parathalassinae *in situ*. **1.** Male of *Parathalassius blasigii* Mik resting on coastal sand dunes at Park Natural do Litoral Norte, Portugal (photo by Rui Andrade). **2.** Female of *Thalassophorus spinipennis* Saigusa resting on intertidal rock along the coast of Rishiri Island, Japan (photo by Masahiko Satô).

## Material & methods

This study is based on the examination of specimens that are deposited in the following institutions: Australian National Insect Collection, Canberra, Australia (ANIC); Canadian National Collection of Insects, Ottawa, Canada (CNC); Essig Museum of Entomology, University of California, Berkeley, USA (EMEC); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBC); Los Angeles County Natural History Museum, Los Angeles, USA (LACM); Lyman Entomological Museum, Ste-Anne-de-Bellevue, Canada (LEMQ); Museo Nacional de Historia Natural, Santiago, Chile (MNHNS); Muséum d'Histoire Naturelle, Geneva, Switzerland (MHNG); Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS); University of Guelph Insect Collection, Guelph, Canada (UGIC); United States National Museum of Natural History, Washington D.C., USA (USNM); Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK); Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZIN); and the Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (ZMHB).

Adult parathalassine specimens are uncommon in collections, but can be collected by sweeping low over coastal, river and riparian habitats. They are not commonly found in mass trapping residues, particularly Malaise traps, but can be taken in yellow pan traps placed directly on river, stream and coastal substrates. Occasionally a particular species (*e.g.*, *Parathalassius sinclairi* Brooks & Cumming) may even be found in abundance in an appropriate microhabitat (see Brooks & Cumming 2017).





**FIGURES 3–11.** Habitus photographs of pinned museum specimens of Parathalassinae. **3.** Male of *Microphorella similis* Brooks. **4.** Male of *Microphorella* Nearctic sp. 6 (*chiragra* group). **5.** Male of *Microphorella* Nearctic sp. 10. (short  $R_1$  group). **6.** Male of *Microphorella malaysiana* Shamshev & Grootaert (*malaysiana* group). **7.** Male of *Plesiothalassius natalensis* Ulrich. **8.** Male holotype of *Neothalassius triton* Brooks & Cumming. **9.** Male holotype of *Microphorella vockerothi* Brooks & Cumming (*chillcotti* group). **10.** Male of *Eothalassius borkenti* Cumming & Brooks. **11.** Female of *Chimerothalassius runyoni* Brooks & Cumming.

As in our previous papers (e.g., Brooks & Cumming 2011, 2012, 2016, 2017, 2018), terms used for adult structures primarily follow Cumming & Wood (2009, 2017). Homologies of the male terminalia follow Brooks & Cumming (2011, 2012, 2016, 2017, 2018) and Brooks & Ulrich (2012).

Seventy-nine morphological characters were used in the phylogenetic analysis, including 63 binary and 16 multistate characters (see “Phylogenetic analysis”). All characters were equally weighted and treated as unordered. Characters were scored for 40 ingroup taxa and two outgroup taxa (Table 2). Ingroup taxa consisted of exemplars from all known extant genera, species groups and newly discovered undescribed lineages of Parathalassinae, worldwide, as well as *Microphor* Macquart and *Schistostoma* Becker from the Microphorinae, and two genera of Dolichopodidae *s.str.* Representative specimens of all exemplar taxa were examined (Table 1), except for *Microphorella emiliae* Shamshev, *Eothalassius gracilis* Shamshev & Grootaert and *E. platypalpus* Shamshev & Grootaert, which were scored using original descriptions from the literature (i.e., Shamshev 2004 and Shamshev & Grootaert 2005). The two outgroup taxa selected for the analysis were single exemplar species in the brachystomatid genera *Anomalempis* Melander (Brachystomatinae) and *Apalocnemis* Philippi (Trichopezinae). Character polarity was determined by rooting the tree with the two outgroups, which together were constrained to be paraphyletic in relation to the ingroup. Parsimony analysis of the character state matrix (Table 2) was performed using PAUP\* version 4.0b10 (Swofford 2002). A heuristic search using stepwise addition, random addition sequence of taxa and tree-bisection-reconnection (TBR) branch swapping with a 1000 random replications, was conducted to find the most parsimonious trees. Tree statistics such as consistency index (CI), retention index (RI), and rescaled consistency index (RC) were calculated to assess the fit of data to the cladograms. Character state distributions were examined using MacClade version 4 (Maddison & Maddison 2003).

## Phylogenetic analysis

The phylogenetic analysis was based on exemplars of all world generic and subordinate level groups of Parathalassinae currently known to us, plus those of Microphorinae and Dolichopodidae *s.str.*, as well as two outgroup taxa (Table 1, Figs 12–15). The characters and character state codings used in the analysis are listed below and appear in the character matrix (see Table 2).

### Head

1. *Clypeus*: separated from face by suture (0); not separated from face, suture indistinct (1).
2. *Gena development*: weakly produced and narrow below compound eye (0); strongly produced and widened below eye (1).
3. *Mouthpart orientation*: directed ventrally (0); directed posteroventrally (1).
4. *Epipharyngeal blades*: narrow (0); heavily sclerotized (1).
5. *Epipharyngeal carina*: small (0); enlarged (1).
6. *Male palpus length*: short (0); long (1).
7. *Male palpus shape*: narrow (0); oval/clavate (1); flattened (2); triangular with pointed apex (3).
8. *Palpus sensory pit*: absent (0); present (1).
9. *Pseudotracheae number*: more than 6 (0); 6 or less (1).
10. *Pseudotracheae form*: rings (0); geminate (1).
11. *Stylus*: two-articles (0); one-article (1).
12. *Stylus length*: normal (0); lengthened (1); very short (2).
13. *Antennal position*: placed at or below middle of head (0); placed above middle of head (1).
14. *Male eye separation*: holoptic (0); dichoptic (1).
15. *Male face*: broad (0); narrow (1).
16. *Eye*: bare (0); with ommatrichia (1).
17. *Position of fronto-orbital setae*: pair arising near base of antennae (0); pair arising near ocelli (1).

### Thorax

18. *Transverse ventrocervical sclerite*: absent (0); present (1).
19. *Presternum shape*: ventral portion narrow (0); ventral portion broad (1).
20. *Prosternum*: separate (0); broadly fused forming precoxal bridge (1).



21. *Strong postpronotal seta*: present (0); absent (1).
22. *Scutellar setae*: two or more pairs (0); one pair (1).
23. *Notum*: without prescutellar depression (0); with prescutellar depression (1).

## Legs

24. *Fore coxa basal bristle(s)*: absent (0); present (1).
25. *Fore coxa blunt spines*: absent (0); present (1).
26. *Male hind trochanter*: without spine-bearing tubercle (0); with spine-bearing tubercle (1).
27. *Fore and/or hind tarsomere 1 base*: without spinose anterior tubercle (0); with spinose anterior tubercle (1).
28. *Male mid tarsomere 1*: without ventral row of hook-like setae (0); with ventral row of hook-like setae (1).
29. *Male hind tarsus*: unmodified (0); swollen, flattened or enlarged (1).
30. *Tarsomere 5 finger-like medial process*: absent (0); present (1).

## Wing

31. *Costa termination*: circumambient (0); ending before posterior margin of wing (1).
32. *Costal vestiture*: simple setae (0); single row of spine-like setae (1); double row of spine-like setae (2).
33. *Costal spine-like setae proximal to R<sub>1</sub>*: not larger and more widely spaced (0); larger and more widely spaced (1).
34. *Costal spines on base of wing*: absent (0); present (1).
35. *Sc*: complete reaching costa (0); complete but faint apically (1); apically reduced or fused to R<sub>1</sub> (2).
36. *R<sub>1</sub> termination*: beyond midpoint of wing (0); before midpoint of wing (1).
37. *Pterostigma*: present (0); absent (1).
38. *Rs origin*: distal (0); opposite humeral crossvein (1).
39. *Crossvein bm-m*: complete (0); incomplete (1); absent (2).
40. *Crossvein dm-m*: present (0); anterior part absent (1); posterior part absent (2); entirely absent (3).
41. *M<sub>2</sub>*: present (0); absent (1).
42. *Shape of CuA*: truncate (0); recurved (1); arched (2).
43. *CuA+CuP*: present beyond cell cua (0); absent or vestigial beyond cell cua (1).
44. *Anal lobe*: strongly developed (0); weakly developed (1).
45. *Male wing margin*: long apicoventral seta absent (0); long apicoventral seta present (1).

## Male abdomen

46. *Male abdominal sternite 1 nipple-like process*: absent (0); present (1).
47. *Male sternite 5*: not projected (0); ventrally projected (1).
48. *Male pregenital segments*: unmodified (0); segment 7 tubular (1).
49. *Male tergite 7 vestiture*: setose (0); bare or with only a few scattered setulae (1).
50. *Male tergite 8*: rectangular (0); slender (1); absent (2).
51. *Male sternite 8*: small (0); widened (1); hypertrophied (2).
52. *Male genitalia rotation*: unrotated (0); rotated between 90-180 degrees and lateroflexed to right (1).
53. *Epandrium and hypandrium*: separate with margins defined (0); partially fused (1); fused together to form capsule (2).
54. *Hypopygial foramen*: absent (0); present (1).
55. *Epandrial lamellae*: basally or nearly basally connected (0); widely separated (1).
56. *Left epandrial lamella*: without ventral process (0); with ventral process (1).
57. *Left ventral epandrial process*: unarticulated (0); articulated (1).
58. *Shape of left ventral epandrial process*: unbranched (0); Y-shaped (1); bifurcate (2).
59. *Right epandrial lamella*: without ventral process (0); with ventral process (1).
60. *Right epandrial lamella shape*: not emarginate dorsally (0); deeply emarginate dorsally (1).
61. *Surstyli*: without prensisetae (0); with prensisetae (1).
62. *Hypandrium*: with long setae present (0); bare (1); with short setae present (2).
63. *Elongate medial hypandrial projection*: absent (0); present (1).
64. *Postgonites*: similar size (0); right postgonite enlarged (1); left postgonite enlarged (2).

65. *Phallus*: mainly straight (0); directed upwards away from hypandrium (1).
66. *Ejaculatory apodeme*: small and rod-like (0); large and expanded (1).
67. *Hypoproct*: weakly projected (0); strongly projected (1).
68. *Proctiger*: right and left cercus of similar size (0); right cercus enlarged (1).

#### Female abdomen

69. *Apical female abdominal segments*: retracted into segment 7 or 8 (0); retracted into segment 6 or 5 (1).
70. *Female tergite 5*: without cluster of stout marginal setae (0); with cluster of stout marginal setae (1).
71. *Female tergite 6*: without row of robust marginal setae (0); with robust marginal setae (1).
72. *Female tergite 8*: entire (0); posterior margin with deep cleft (1); completely divided medially (2).
73. *Spermathecal receptacle*: spherical, sclerotized and darkly pigmented (0); tubular, unsclerotized and unpigmented (1); coiled tube (2).
74. *Female cercus*: narrow and pointed (0); broadly rounded (1); with elongate, narrow, apical projection (2).
75. *Female cercus sclerotization*: heavily sclerotized (0); lightly sclerotized (1).
76. *Female tergite 10*: with acanthoporous spines (0); with acanthoporous spines and setae (1); with acanthoporous setae (2).
77. *Female tergite 10*: divided medially (0); undivided (1).
78. *Female sternite 10*: not narrowed into pair of bands (0); narrowed into pair of elongate bands (1).
79. *Female segment 10*: tergite and sternite widely separated (0); tergite and sternite articulated (1).

The phylogenetic analysis resulted in two most parsimonious trees (length = 215, CI = 0.46, RI = 0.76, RC = 0.35). These two trees varied only in the placement of *Microphorella curtipes* (Becker), as depicted in the strict consensus tree (Fig. 12). One of the two cladograms was selected to show the character state distributions (Figs 13–14). In this tree *M. curtipes* is sister to the *Microphorella acroptera* group + *Microphorella s.str.* + *Parathalassius* based on homoplastic character state 47.1 (Fig. 14), whereas in the other tree (not shown) it is sister to the *Microphorella chiragra* group based on homoplastic character state 51.1.

The analysis corroborates the monophyly of the Microphorinae + Dolichopodidae *s.str.* + Parathalassiinae based on 10 synapomorphies (Fig. 13) as depicted by Sinclair & Cumming (2006). It also once again confirms the sister group relationship of the Dolichopodidae *s.str.* and the Parathalassiinae based on 18 synapomorphies (involving mouthparts, antenna, head, thorax, wing, male genitalia and female terminalia), the strongest supported node in the analysis. This is why the Parathalassiinae cannot be combined together with the Microphorinae into a single subfamily, or family, as is still practiced by some authors (*e.g.*, Yang *et al.* 2007). The monophyly of the Parathalassiinae is clearly supported by three non-homoplastic synapomorphies, namely a one-articled stylus (11.1), lack of a strong postpronotal seta (21.1) and the left epandrial lamella of the male genitalia with a ventral process (56.1).

Within the Parathalassiinae, the South African lineage that includes two distinctive genera (*Amphithalassius* and *Plesiothalassius*) is supported by 7 derived character states, of which one, a lightly sclerotized female cercus (75.1), is non-homoplastic. This lineage is sister to the remainder of the Parathalassiinae, which as a group is supported as monophyletic by four synapomorphies. Two of these, namely a narrow male face (15.1) and widely separated epandrial lamellae of the male genitalia (55.1), are uniquely derived. This large lineage currently contains 6 genera plus *Microphorella*, which itself includes 12 separate groups (Fig. 15). The entire lineage is divided into two clades, the first of which includes *Neothalassius* + Undescribed New Caledonia genus + *Chimerothalassius* + *Microphorella* short  $R_1$  group + *Eothalassius*. This diverse clade is supported by only a single character state, a short vein  $R_1$  that terminates before the midpoint of wing (36.1) (Fig. 13). The second clade, which includes *Thalassophorus* + 11 distinct *Microphorella*-like groups + *Parathalassius* is also supported by a single character state, a sensory pit on the palpus (8.1) (Fig. 14).

The clade that includes *Neothalassius* + Undescribed New Caledonia genus + *Chimerothalassius* + *Microphorella* short  $R_1$  group + *Eothalassius*, is divided into two groups (Fig. 13). *Neothalassius* + Undescribed New Caledonia genus + *Chimerothalassius* all have a derived medial process on tarsomere 5 of each leg (30.1) and have entirely lost wing veins dm-m (40.3) and  $M_2$  (41.1). Undescribed New Caledonia genus shares a long male palpus (6.1) and vestigial CuA+CuP vein (43.1) with *Chimerothalassius*, but has acanthoporous spines rather than acanthoporous setae on the female terminalia (76.2). *Microphorella* short  $R_1$  group and *Eothalassius* share modified male genitalia with the epandrium and hypandrium partially fused together (53.1) and female terminalia with tergite

10 and sternite 10 widely separated (79.0). *Eothalassius* is a distinctive genus with a flattened male palpus (7.2), lengthened antennal stylus (12.1) and a setose hypandrium in the male (62.2). *Microphorella merzi* Gatt is placed within *Eothalassius* by the analysis and is herein treated as a member of the genus (see below under “Preliminary classification of the Parathalassiinae”).

The clade that includes *Thalassophorus* + 11 distinct *Microphorella*-like groups + *Parathalassius* is shown on Figure 14. *Thalassophorus* + *Microphorella malaysiana* + *Microphorella* South Africa species + *Microphorella emiliae* are positioned at the base of this clade primarily because these taxa have the female terminalia with acanthoporous setae rather than acanthoporous spines (76.0), the single homoplastic character state that unites the rest of the clade. This character is possibly subjected to selection pressures with differing oviposition behaviours. *Microphorella emiliae* and *Thalassophorus* also share a uniquely derived triangular shaped palpus (7.3), which partially supports them as sister taxa. The remaining *Microphorella*-like groups + *Parathalassius* lineage contains a few individual species (or species pairs) and several very distinctive groups. These include the *Microphorella chillcotti* group defined by two uniquely derived states, namely the male wing bearing a long apicoventral seta (45.1) and an enlarged right postgonite on the male genitalia (64.1), as well as six other synapomorphies. The *Microphorella chiragra* group is characterized by a setose hypandrium in the male (62.2) and uniquely derived robust marginal setae on female tergite 6 in at least the exemplar species analysed (71.1). The *Microphorella acroptera* group is partially defined by a non-homoplastic spine-bearing tubercle on the male hind trochanter (26.1) and females of most species with a uniquely derived cluster of stout median setae on tergite 5 (70.1). *Microphorella s.str.*, which includes the type species *M. praecox* (Loew) and several other species, including *M. similis* Brooks & Ulrich, is characterized by 11 synapomorphies and is the best supported species group/genus level taxon in the subfamily. It is the sister group to *Parathalassius* with both sharing four synapomorphies, including the uniquely derived deeply emarginate right epandrial lamella (60.1) and enlarged left postgonite (64.2) of the male genitalia. *Parathalassius* itself is characterized by two or more pairs of scutellar setae (22.0) and a truncate CuA vein (42.0), two apparent reversals.

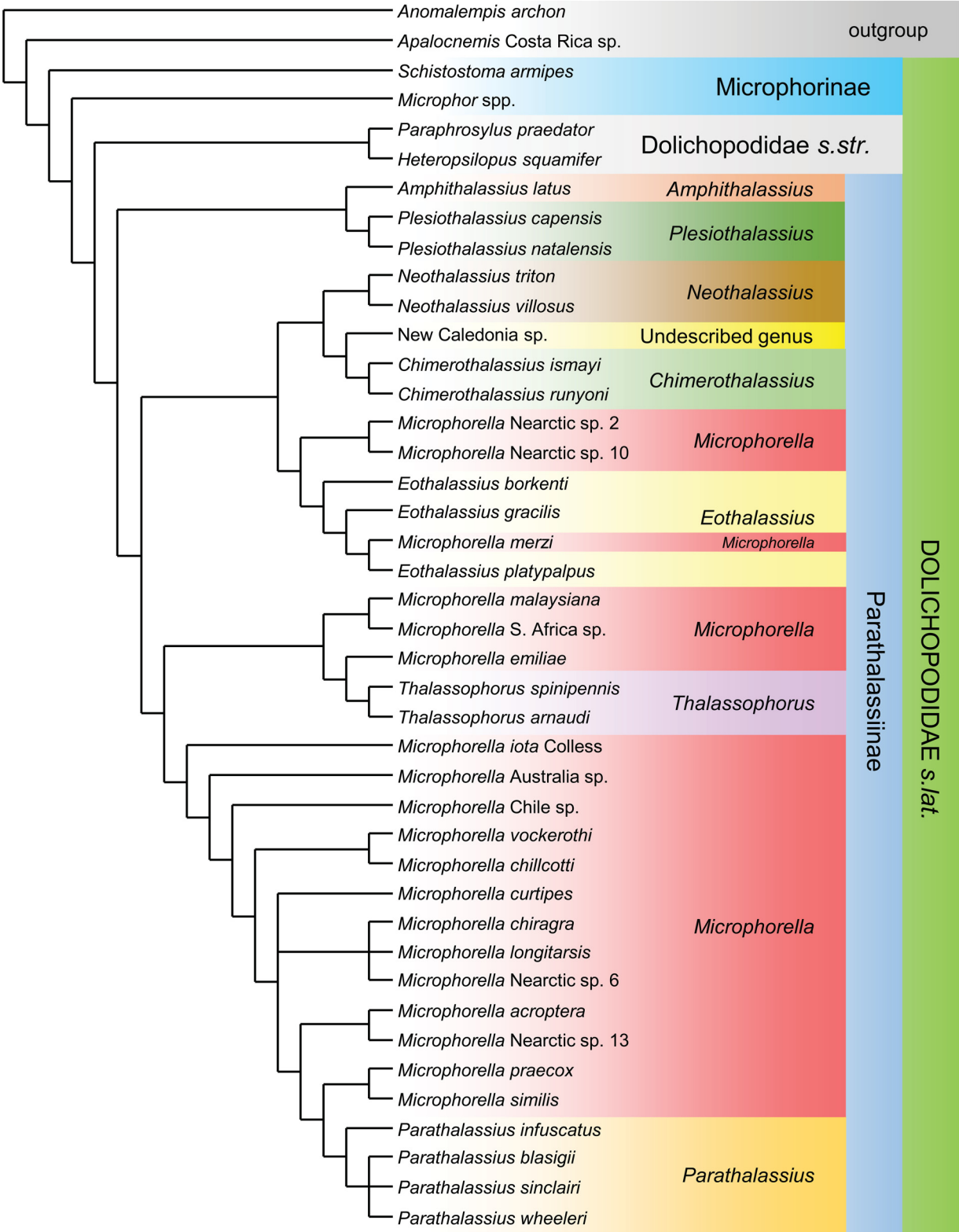
### Preliminary classification of the Parathalassiinae

Based on the phylogenetic analysis and known distribution patterns, 20 distinctive subgroups of Parathalassiinae (genera and species groups of *Microphorella*) can currently be recognized. Each of these groups is outlined and briefly diagnosed below with all included described and undescribed species known to us. The groups are listed in the same order that they appear in Figure 15.

**Genus *Amphithalassius* Ulrich.** A South African genus that includes two described species (*A. latus* Ulrich and *A. piricornis* Ulrich) and three undescribed species known only from females. The genus is characterized by a whitish pruinose body, conical apically tapered postpedicel, wide parallel-sided face in both sexes, palpus with a sensory pit, irregular uniserial acrostichal setae, male abdominal sternite 5 ventrally projected, compact male genitalia with cerci of similar size, and female terminalia with acanthoporous setae. The closely related South African genus *Plesiothalassius* is similar but has a globular apically rounded postpedicel, narrower face with sides curved inward near middle, palpus without sensory pit, biserial acrostichals, male abdominal sternite 5 not projected, and male right cercus enlarged. *Amphithalassius* and *Plesiothalassius* are also distinguished in the key to Afrotropical Dolichopodidae provided by Grichanov & Brooks (2017). Ulrich (1991) provides a key to the known species. Adults occur along sea coasts on dry sand and dunes with sparse vegetation.

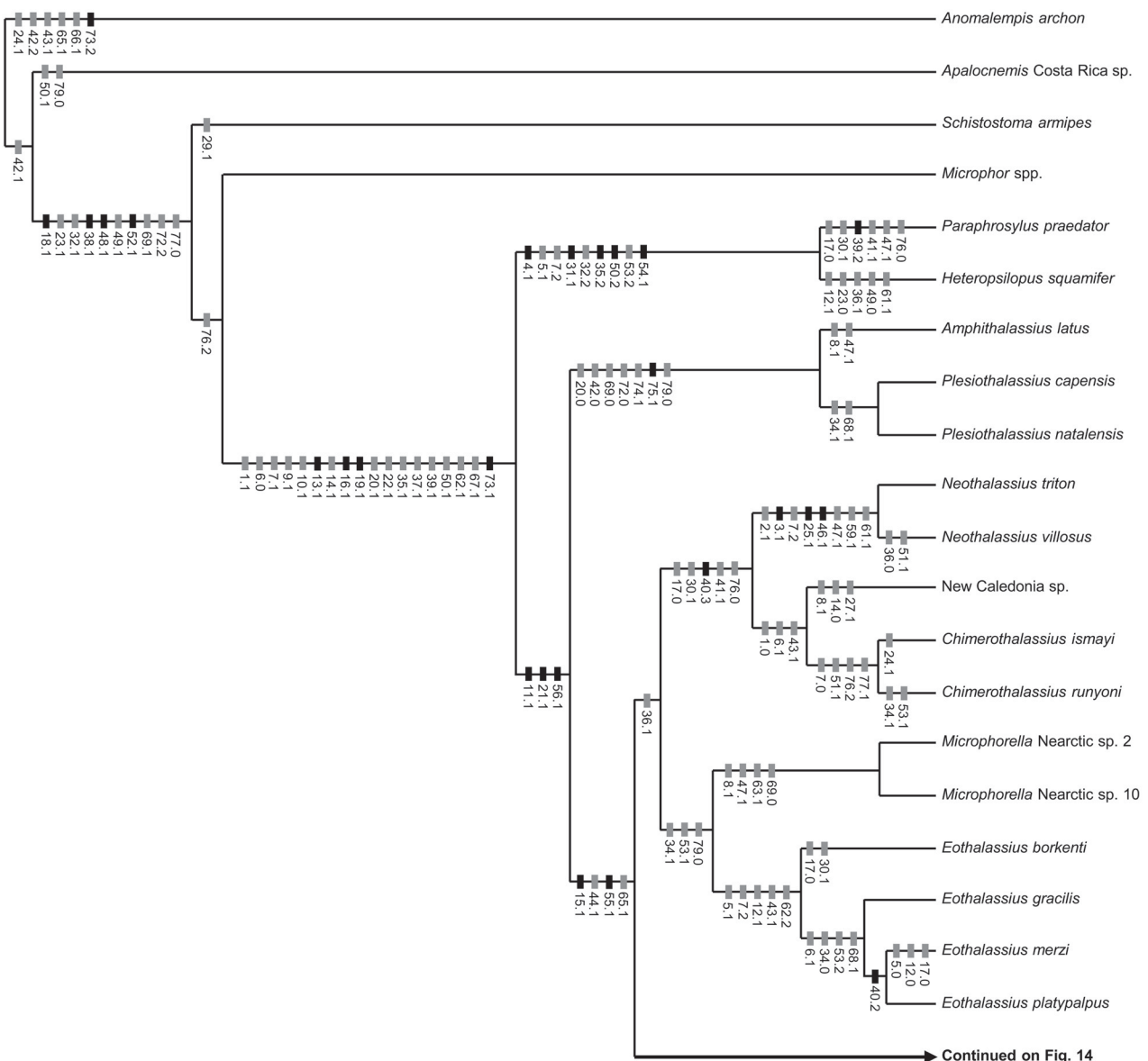
**Genus *Plesiothalassius* Ulrich** (Fig. 7). A South African genus that includes three described species, *P. capensis* (Smith), *P. flavus* Ulrich and *P. natalensis* Ulrich. *Plesiothalassius* is very similar to *Amphithalassius* (see above section for diagnostic features of both genera). Ulrich (1991) provides an identification key to the described species. Adults occur along sea coasts on dry sand and dunes with sparse vegetation (Grichanov & Brooks 2017).

**Genus *Neothalassius* Brooks & Cumming** (Fig. 8). A genus that includes two described species (*N. triton* Brooks & Cumming and *N. villosus* Brooks & Cumming) from the rocky seashores of Chile and Peru. *Neothalassius* is easily characterized by the mouthparts directed posteroventrally and with a broad flat palpus, wing veins dm-m and M<sub>2</sub> absent, fore coxa spinose, and male with a nipple-like process on abdominal sternite 1. Brooks & Cumming (2016) provide an identification key to males.



**FIGURE 12.** Strict consensus tree of the two most parsimonious cladograms produced by the phylogenetic analysis of the data matrix in Table 2 with current genera of Parathalassinae and family-group divisions of Dolichopodidae indicated.





**FIGURE 13.** One of the two most parsimonious trees (in part) produced by the phylogenetic analysis of the data matrix in Table 2 (tree continued in Fig. 14). Character state distributions for uniquely derived states are indicated by black hash marks and homoplastic states are indicated by grey hash marks.

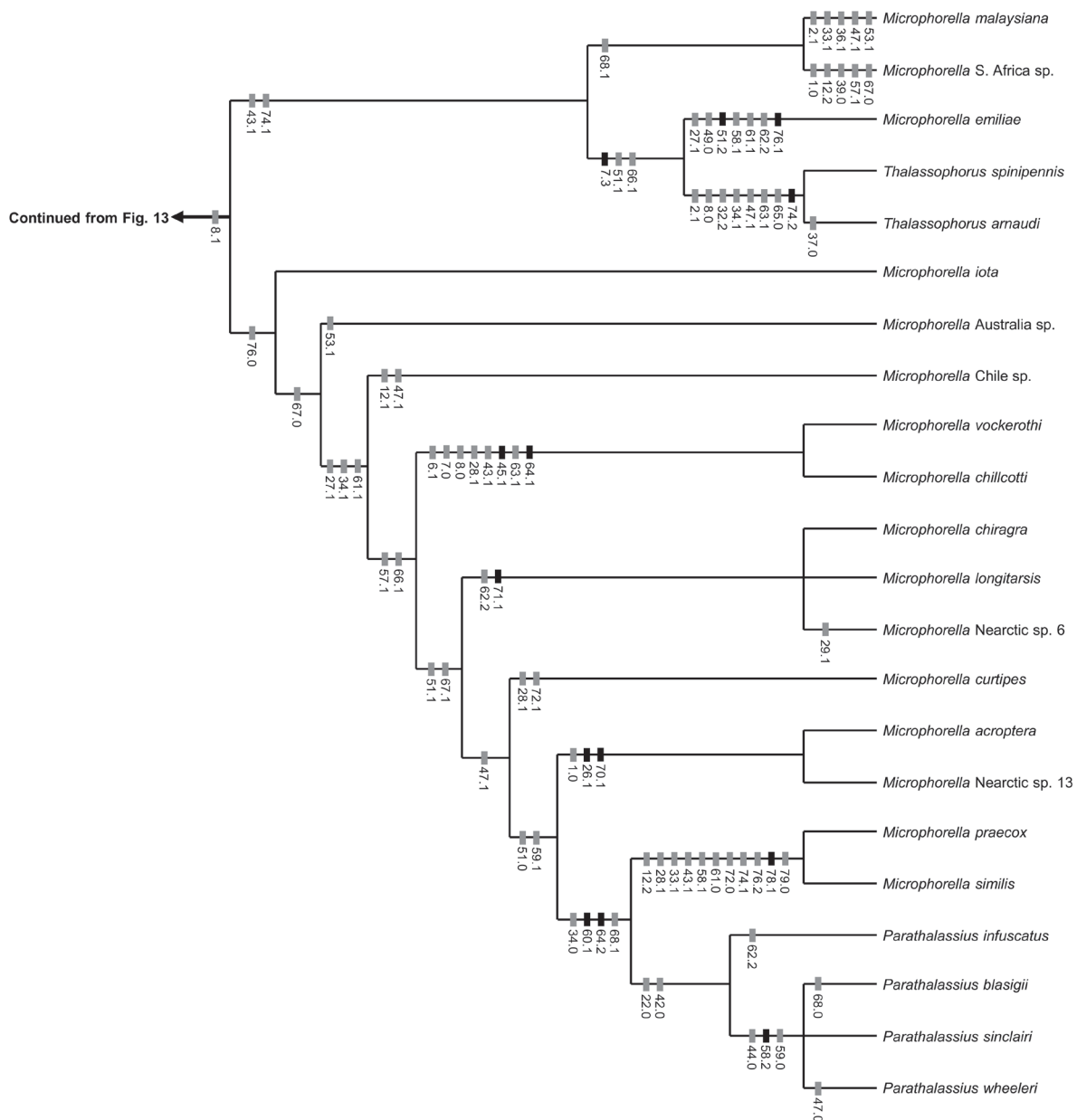
**Undescribed genus (New Caledonia).** This group includes two undescribed species from New Caledonia that are somewhat intermediate in features between *Neothalassius* and *Chimerothalassius* (Brooks & Cumming 2018). All three genera have the same derived wing venation (veins dm-m and  $M_2$  absent), but most importantly, unlike *Chimerothalassius*, the New Caledonia genus has the female terminalia with tergite 10 divided and bearing acanthophorous spines. Adults of both species were collected on emerged rocks in a river.

**Genus *Chimerothalassius* Shamshev & Grootaert** (Fig. 11). *Chimerothalassius* includes two described species, *C. ismayi* Shamshev & Grootaert from New Zealand and *C. runyoni* Brooks & Cumming from the Caribbean, and three undescribed species (two from New Zealand and one from Costa Rica) (Brooks & Cumming 2018). This odd generic distribution may represent an old relict Tertiary pattern as discussed by Brooks & Cumming (2011, 2018). *Chimerothalassius* has wing veins dm-m and  $M_2$  absent like the previous two genera, but the female terminalia have tergite 10 undivided (versus divided) and bearing acanthophorous setae (versus spines). The genus is also characterized by an elongate, narrow palpus. *Chimerothalassius* appears to be restricted to rocky or stony habitats of coastal beaches (Shamshev & Grootaert 2002; Brooks & Cumming 2018).

***Microphorella* short  $R_1$  species group** (Fig. 5). This group includes three undescribed species from western North

America that all share a short  $R_1$  vein. This feature is seen in some other parathalassiines (e.g., *Neothalassius*, *Chimerothalassius*, *Eothalassius*) but not in groups that currently would be classified within *Microphorella* (except the *M. malaysiana* group). The group is also characterized by several features found in other parathalassiines, namely a palpus with a sensory pit, male abdominal sternite 5 projected ventrally, an elongate medial hypandrial projection of males, and extensive retraction of the apical female abdominal segments. In addition, like *Eothalassius*, *C. runyoni*, the *M. malaysiana* group and the *Microphorella* South Africa species, the short  $R_1$  group has the epandrium and hypandrium partially fused together. The three included species are found along fast flowing rivers and streams.

**Genus *Eothalassius* Shamshev & Grootaert** (Fig. 10). This distinctive genus was described by Shamshev & Grootaert (2005) for two species from Southeast Asia and Papua New Guinea (*E. gracilis* Shamshev & Grootaert and *E. platypalpus* Shamshev & Grootaert), and later expanded by Brooks & Cumming (2011) to include another species (*E. borkenti* Cumming & Brooks) from Costa Rica. Both sets of authors also suggested that the Mediterranean species *Microphorella merzi* Gatt probably belongs in *Eothalassius*. Since the cladistic



**FIGURE 14.** One of the two most parsimonious trees (in part) produced by the phylogenetic analysis of the data matrix in Table 2 (tree continued from Fig. 13). Character state distributions for uniquely derived states are indicated by black hash marks and homoplastic states are indicated by grey hash marks.

analysis confirms this placement (Figs 12, 13), *Microphorella merzi* Gatt is hereby classified in *Eothalassius* Shamshev & Grootaert, as *Eothalassius merzi* (Gatt) **comb. nov.** (Fig. 15). There is also one undescribed species from New Caledonia and two from Japan. In addition to a short  $R_1$  vein plus the epandrium and hypandrium partially fused together in the male (features shared with some other groups), the genus is also characterized by a large flattened palpus, a lengthened antennal stylus, wing vein CuA+CuP absent, and male genitalia with a setose hypandrium. Most species of *Eothalassius* are known from sandy or rocky coastal beaches, but both Japanese species were collected along forest streams.

***Microphorella malaysiana* species group** (Fig. 6). Besides *M. malaysiana* Shamshev & Grootaert, this group also includes *M. bira* Shamshev & Grootaert, *M. papuana* Shamshev & Grootaert and *M. satunensis* Shamshev & Grootaert, which are all known from sea coasts in Southeast Asia. Shamshev & Grootaert (2004) provide a key to the species. The group is characterized by a short  $R_1$  wing vein, male abdominal sternites 5 and 6 projected ventrally, male genitalia with the epandrium and hypandrium partially fused together, and female terminalia with acanthoporous setae on tergite 10 and a broadly rounded cercus. Shamshev & Grootaert (2004) also mention that males possess a sexually dimorphic pale coloured palpus and genitalia endowed with a massive right surstylar lobe.

***Microphorella* South Africa species group.** This “group” includes a single undescribed species from the Western Cape Province of South Africa. It possesses a very short antennal stylus, wing with crossvein bm-m complete, and males with modified leg chaetotaxy including a curled cluster of long setae on the fore trochanter, a long posterior bristle on the fore tibia and a long bristle on the mid trochanter. The male genitalia possess an articulated left ventral epandrial process and weakly projected hypoproct. The specimens were collected in a Malaise trap in an inland meadow at 300 m elevation and are the first known non-coastal parathalassiines from the Afrotropical Region.

***Microphorella emiliae* species group.** This “group” includes a single very distinctive species from Far East Russia (Sakhalin and Kuril Islands). Both sexes have a triangular shaped palpus and unique terminalia, with males possessing a hypertrophied sternite 8, and females possessing both acanthoporous setae and spines (single pair) on tergite 10. According to Shamshev (2004) this species was collected along the sea coast in dune grass (*Elymus mollis* Trinius, Poaceae).

**Genus *Thalassophorus* Saigusa** (Fig. 2). A genus with two described species, one from Hokkaido, Japan (*T. spinipennis* Saigusa) and the other from western North America (*T. arnaudi* Brooks & Cumming). *Thalassophorus* is characterized by a well developed gena, triangular shaped palpus without a sensory pit, costa with strong basal spines and a double row of short spine-like setae, male abdominal sternite 5 projected ventrally, male genitalia with an elongate medial hypandrial projection and a straight phallus, female terminalia with acanthoporous setae on tergite 10 and a cercus with a narrow elongate apical projection. The genus appears to be restricted to rocky or stony coastal shorelines (Saigusa 1986; Brooks & Cumming 2011).

***Microphorella iota* species group.** This “group” includes the only described species from Australia (Australian Capital Territory and New South Wales). Males have club-tipped processes on the dorsal surface of the palpus and a phallus with a modified brush-like apex. Colless (1963) states that specimens of *M. iota* were all collected sweeping near streams.

***Microphorella* Australia species group.** An undescribed species from New South Wales (Warrumbungle National Park) was scored in the analysis for this group, which includes another undescribed species from New South Wales (Blue Mountains National Park). Both species were collected along creeks. Females have not been taken of either species. Males have the epandrium and hypandrium partially fused together, unlike *M. iota*, the other Australian group.

***Microphorella* Chile species group.** This “group” includes a single undescribed species from the Maule Region of Chile. It possesses a lengthened antennal stylus, male abdominal sternite 5 projected ventrally, and stout prenisetae on each surstylus of the male genitalia. The specimens were collected along the Corel River.

***Microphorella chillcotti* species group** (Fig. 9). This group includes two described species (*M. chillcotti* Brooks & Cumming and *M. vockerothi* Brooks & Cumming) from western North America. Adults are found on sandy and gravel riverbanks. The *M. chillcotti* group is characterized primarily by a long apicoventral seta on the male wing and an enlarged right postgonite on the male genitalia. Brooks & Cumming (2012) provide a key to the described species and mention the possibility that three additional undescribed species from eastern Asia might also belong to this group.



***Microphorella curtipes* species group.** This group includes the southern European species *M. curtipes* (Becker) that occurs along the *Mediterranean* coast and presumably the central European riparian species *M. beckeri* (Strobl), which Chvála (1988) noted was very similar to *M. curtipes*. The group is characterized by a bulb-shaped postpedicel, male abdominal sternite 5 projected ventrally, and the female terminalia with the posterior margin of tergite 8 deeply cleft. The North African species *Microphorella ulrichi* Gatt also seems referable to this group based on Gatt's (2003) illustrations.

***Microphorella chiragra* species group** (Fig. 4). This group includes three described species (*M. chiragra* Melander, *M. longitarsis* Melander and *M. ornatipes* Melander) and 11 undescribed species all from western North America. Males have a setose hypandrium with short setae and females of most species have robust marginal setae on tergite 6. All species collected to date are found along streams and creeks as first indicated by Melander (1928).

***Microphorella acroptera* species group.** This group includes two described species (*M. acroptera* Melander and *M. tubifera* Melander) plus nine undescribed species from western North America. Males have a spine-bearing tubercle on the hind trochanter and females of most species have a cluster of stout median setae on abdominal tergite 5. Included species have been taken along the margins of creeks and lakes.

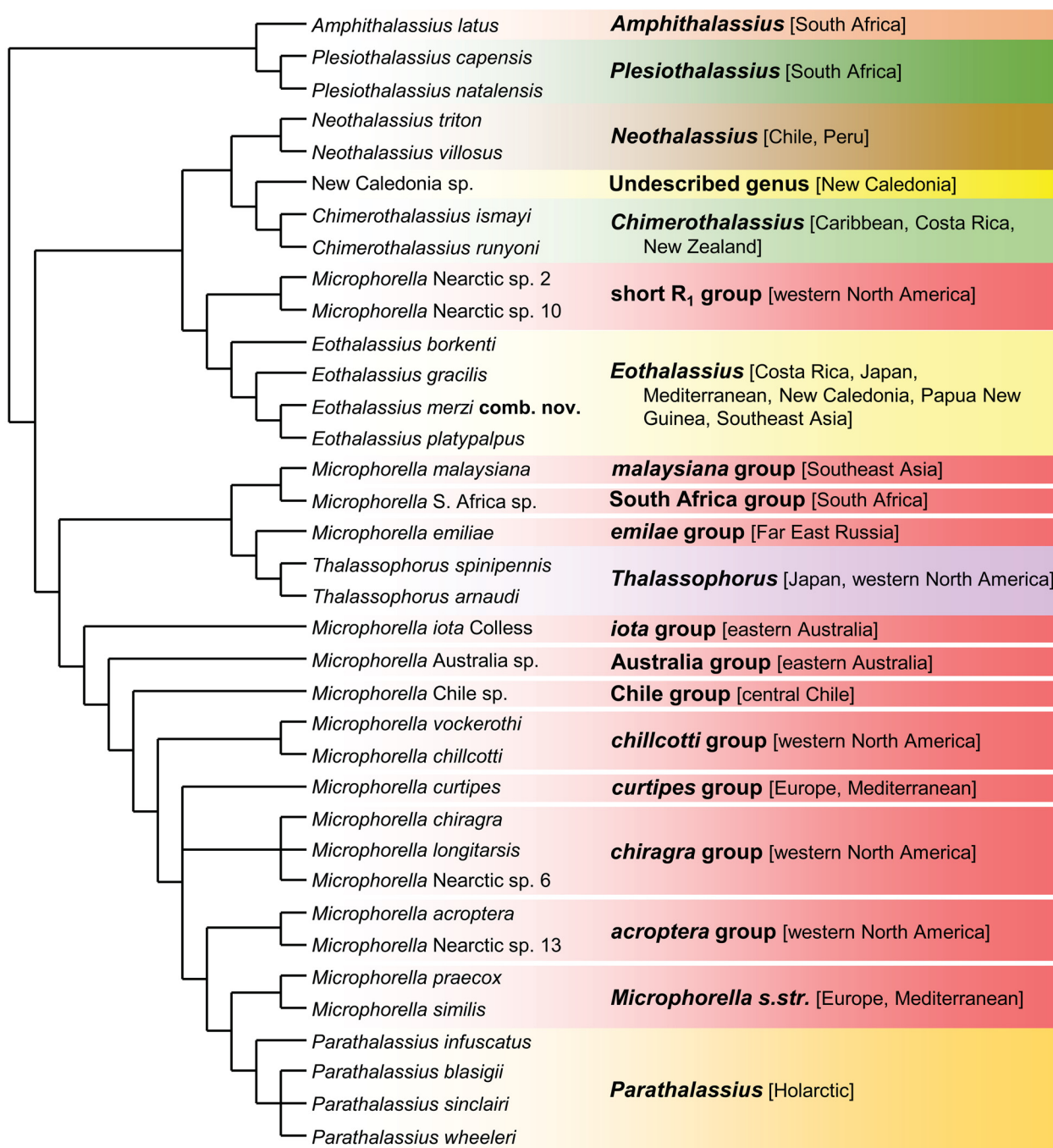
**Genus *Microphorella* s.str.** (Fig. 3). This genus as narrowly defined here, includes the type species *M. praecox* (Loew) and *M. similis* Brooks from Europe (Brooks & Ulrich 2012), as well as *M. cassari* Gatt, *M. ebejeri* Gatt, and *M. mamillata* Gatt from the Mediterranean (Gatt 2011, 2012). *Microphorella praecox* and *M. similis* have been collected on sandy and gravel riverbanks (Brooks & Ulrich 2012), whereas the Mediterranean species are known from coastal shorelines (Gatt 2011, 2012). Additional undescribed species from the Mediterranean are mentioned by Gatt (2012). *Microphorella* s.str. is characterized by a row of hook-like setae on male mid tarsomere 1, wing with large widely spaced costal spine-like setae proximal to R<sub>1</sub>, vein CuA+CuP absent, Y-shaped left ventral epandrial process, and female terminalia with acanthoporous setae on tergite 10, sternite 10 narrowed into pair of elongate bands and a broadly rounded cercus.

**Genus *Parathalassius*** (Fig. 1). This genus includes 15 described species that are found along sandy sea coasts in both the Palaearctic and Nearctic Regions (Brooks & Cumming 2017). The Palaearctic fauna includes *P. blasigii* Mik, *P. maritimus* Shamshev and *P. ulrichi* Shamshev, whereas the Nearctic fauna includes *P. abela* Brooks & Cumming, *P. aldrichi* Melander, *P. candidatus* Melander, *P. dilatus* Brooks & Cumming, *P. infuscatus* Brooks & Cumming, *P. melanderi* Cole, *P. midas* Brooks & Cumming, *P. sinclairi* Brooks & Cumming, *P. socali* Brooks & Cumming, *P. susanae* Brooks & Cumming, *P. uniformis* Brooks & Cumming and *P. wheeleri* Brooks & Cumming. Brooks & Cumming (2017) provide a key to the described species. There appear to be few more undescribed species in both regions. The genus was fully diagnosed and described by Brooks & Cumming (2017) and is most easily recognized by its grey pruinose body coloration, two or more pairs of scutellar setae and a truncate CuA wing vein.

## Discussion

Earlier unpublished analyses and discussions of relationships within the Parathalassiinae (Cumming & Brooks 2006; Brooks & Cumming 2010, 2011, 2016, 2017) have similarly hypothesized placement of the South African genera (*i.e.*, *Amphithalassius* + *Plesiothalassius*) as the sister group to the rest of the subfamily (Figs 13, 14). However, those earlier, less rigorous studies suggested a different set of relationships among the genera within the remaining large clade, to those shown here. In particular, *Parathalassius*, which is partially characterized by two or more pairs of scutellar setae and a truncate CuA vein, is no longer considered the basal lineage in this large clade with these two features now considered apparent reversals. This is largely a result of the strongly supported sister group relationship between *Parathalassius* and *Microphorella* s.str. based on four synapomorphies, including the uniquely derived deeply emarginate right epandrial lamella and enlarged left postgonite of the male genitalia (Fig. 14). Retention of these two names at the generic level may eventually require similar ranks for many of the other included groups. This will probably mean recognition of all other included genera, plus the description of a number of additional genera (or subgenera) for the various *Microphorella* species groups and the Undescribed genus from New Caledonia (Fig. 15). Conversely, synonymizing *Microphorella* with *Parathalassius* (the older name) and including all the subgroups (with possible recognition of subgenera) in a very large *Parathalassius*, would create a very weakly

diagnosable and heterogeneous genus concept. Alternately combining some of the various groups into larger genera appears difficult because of potential paraphyly and the inability to easily characterize each group without using genitalic characters.



**FIGURE 15.** Parathalassiinae portion of the strict consensus tree produced by the phylogenetic analysis of the data matrix in Table 2 with subgroups (genera and species groups of *Microphorella*) and geographic distribution indicated.

However, we consider formal description of a number of additional genera (or subgenera) to be premature and will continue at this point, to recognize various species groups within an open-ended, non-monophyletic, concept of “*Microphorella*” (see Bickel 2009). Recent collecting efforts in the Nearctic Region (see for example, Brooks & Cumming 2011, 2012, 2017, 2018) have revealed a huge increase in Parathalassiinae diversity and it is expected that at least a similar level of diversity remains to be discovered in other zoogeographic regions. Similar collecting efforts from these regions will undoubtedly test the phylogenetic relationships proposed here. In addition, collec-

tion of fresh specimens will allow for phylogenetic analyses of molecular data to be included, further testing the relationships presented here.

Future studies of the Parathalassiinae should focus on discovery of new taxa in all areas of the world. Collaboration by international specialists who collect small flies along shorelines (both freshwater and marine) and in riparian habitats is encouraged. Freshly collected specimens should also be preserved in a manner that will allow for future analysis of molecular data. Additional revisionary work on the distinctive subgroups of Parathalassiinae recognized here is required, particularly all the various species groups currently classified within “*Microphorella*”.

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**TABLE 1.** Exemplar taxa scored in the analysis.

Taxon	Collection Locality
<b>Brachystomatidae</b>	
Brachystomatinae	
<i>Anomalempis archon</i> Melander	<b>Canada:</b> Yukon Territory: Dempster Highway mile 51, 17–21.vi.1973, G. & D.M. Wood (CNC); Dempster Highway km 155, 950 m, 11–12.vi.1973, D. Lafontaine & G. & M. Wood (CNC). <b>USA:</b> Alaska: Nome area, mile 17 of Kougarak Road, 64°42'22"N 165°17'50"W, 20–26.vi.2005, J. & R. Skevington (CNC).
Trichopezinae	
<i>Apalocnemis</i> Costa Rica sp 1.	<b>Costa Rica:</b> San José, Zurqui de Moravia, 1600 m, x–xi.1990, iii.1991, P. Hanson (CNC).
<b>Dolichopodidae s.lat.</b>	
Microphorinae	
<i>Microphor pilimanus</i> Strobl (male)	<b>Spain:</b> Sierra Nevada Highway, 1850 m, 7.vii.1986, J.R. Vockeroth (CNC).
<i>Microphor</i> sp. (female)	<b>USA:</b> California: Marin Co., Alpine Lake (CNC).
<i>Schistostoma armipes</i> (Wheeler)	<b>Canada:</b> British Columbia: Mission City, 28.vi.1953, W.R.M. Mason & G.J. Spencer (CNC).
Parathalassinae	
<i>Amphithalassius latus</i> Ulrich	<b>South Africa:</b> Western Cape: Nature's Valley, 23.x.1991, H. Ulrich (CNC).
<i>Chimerothalassius ismayi</i> Shamshev & Grootaert	<b>New Zealand:</b> South Island: Cable Bay, 41°09.6'S 173°24.9'E, 13.ii.1998, W.N. Mathis (USNM); Banks Peninsula, Port Levy, 22–26.ii.1999, nr sea streambed, S.A. Marshall (UGIC).
<i>Chimerothalassius runyoni</i> Brooks & Cumming	<b>Dominica:</b> Layou River mouth, 9.i.1965, sea shore, W.W. Wirth (USNM). <b>Montserrat:</b> Woodlands Beach, 16°45.817'N 62°13.384'W, 20–22.vi.2017, rocks in intertidal zone, J.B. Runyon (CNC).
<i>Eothalassius borkenti</i> Cumming & Brooks	<b>Costa Rica:</b> Cabo Blanco, 19.i.1994, tidal rocks, A. Borkent (CNC); Herradura, 25.x.1993/16.xii.1993, tidal rocks, A. Borkent (CNC); Manuel Antonio NP, 17.xi.1993, intertidal zone, A. Borkent (INBC); Corcovado NP, San Pedrillo, 8°37'15"N 83°44'6"E, 14.viii.2001, rocky sea shore M. Buck (UGIC).
<i>Eothalassius gracilis</i> Shamshev & Grootaert	<b>Indonesia:</b> Irian Jaya, Sanoba Beach (Nabire), 21.iv.1997, P. Grootaert (RBINS); Sumatra, Pulau Sirandah, 24.iii.1994, P. Grootaert (RBINS). <b>Papua New Guinea:</b> Madang Province: Laing I., 2–4.iii.1992/6.vi.1994, P. Grootaert (RBINS). <b>Thailand:</b> Phang-Nga Province: Nangtong, Khao Lak, 9.iv.1996, sandy beach, P. Grootaert (RBINS). Specimens not examined.
<i>Eothalassius platypalpus</i> Shamshev & Grootaert	<b>Papua New Guinea:</b> Madang Province: Rivo, along creek, 7.ix.1987, P. Grootaert (RBINS); Mandang beach, 11.viii.1987, P. Grootaert (RBINS); New Ireland Province: Taskiki, sandy beach along creek, 28.iv.1993, P. Grootaert (RBINS). Specimens not examined.
<i>Microphorella acroptera</i> Melander	<b>USA:</b> California: Riverside Co., Thousand Palms, Willis Palms Oasis, 8.iii.1955, W.R. Richards (CNC); 1000 Palms Oasis, 18.iii.1955, W.R. Richards (CNC); San Mateo Co., Jasper Ridge Biological Preserve, 22.iv.1990, P.H. Arnaud (USNM); Oregon: Curry Co., Floras Creek, 42°54'58"N 124°20' 37"W, 29.v.2009, S.E. Brooks (CNC).
<i>Microphorella</i> Australia sp.	<b>Australia:</b> New South Wales: Warrumbungle NP, Buckley's Creek, 12–17.xii.1995, M. Sharkey (CNC).
<i>Microphorella</i> Chile sp.	<b>Chile:</b> Maule Region: Corel River, 35°23'24.3"S 71°15'16.4"W, 314 m, 28.i.2011, D.S. Amorim (CNC).
<i>Microphorella chillcotti</i> Brooks & Cumming	<b>Canada:</b> British Columbia: Exchamsiks River, 58km SW of Terrace, 54°20.00'N 129°17.81'W, 15–18.viii.2008, S.E. Brooks & J.M. Cumming (CNC). <b>USA:</b> Washington: Skagit Co., Cascade River margin, 48°27'54"N 121°13'1"W 1186', 9/17.vi.2018, S.E. Brooks & J.M. Cumming (CNC).
<i>Microphorella chiragra</i> Melander	<b>USA:</b> California: Del Norte Co., West Fork Patrick Creek, 41°55'03"N 123°51'28"W, 24–31.v.2009, J.M. Cumming & S.E. Brooks (CNC).

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TABLE 1. (Continued)

Taxon	Collection Locality
<i>Microphorella curtipes</i> (Becker)	<b>France:</b> Corsica: SW Biguglia, 30.iv.1990, H. Ulrich (CNC).
<i>Microphorella emiliae</i> Shamshev	<b>Russia:</b> , Kunashir (Kuril Islands), Tret'yakovo, 5.ix.1971, sea terraces, E.P. Nartshuk (ZIN); Sakhalin, 10km N Shebunino, 27.v.1968, sea shore, on <i>Elymus mollis</i> , E.P. Nartshuk (ZIN). Specimens not examined.
<i>Microphorella iota</i> Colless	<b>Australia:</b> Australian Capital Territory: Mt. Majura, 2.iv.1962, D.H. Colless (ANIC); Ginninderra Falls 23.ii.1962, D.H. Colless (ANIC).
<i>Microphorella longitarsis</i> Melander	<b>USA:</b> Idaho: Latah Co., 7 mi. N Troy nr Big Meadow Rec. Area, 3000', 13.vii.1979, W.J. Turner (LACM, USNM); Moscow Mtn, 46°47.721'N 116°54.093'W, 22.vi.2014, 1000 m, cascading stream, B.J. Sinclair (CNC); Kootenai Co., Hwy 97, St. Joe NF, FR 438, 47°36.392'N 116°40.099'W, 19.vi.2014, tribs Beauty Creek, B.J. Sinclair (CNC).
<i>Microphorella malaysiana</i> Shamshev & Grootaert	<b>Singapore:</b> Pulau Semakau, 26.vi.2005, P. Grootaert (RBINS).
<i>Microphorella merzi</i> Gatt	<b>Cyprus:</b> 10km W Pissouri, Petra tou Romiou, 34.41°N 32.35°E, 0 m, 23.iv.2002, beach, Merz, Deeming, Ebejer & Gatt (MHNG); 6 km E Zygi, 34°44'44"N 32°44'55"E, 24.iv.2002, beach, P. Gatt (MHNG); Akamas Peninsula, Lara Beach, 34.58°N 32.19°E, 28.iv.2002, dunes, meadow, Merz, Deeming, Ebejer & Gatt (MHNG); Lemasos, Pegasus beach hotel, 34.42°N 33.06°E, 1.v.2002, beach, Merz, Deeming, Ebejer & Gatt (MHNG).
<i>Microphorella</i> Nearctic sp. 2	<b>USA:</b> California: Del Norte Co., West Fork of Patrick Creek, 41°55'03"N 123°51'28"W, 24.v. -3.vi.2009, J.M. Cumming & S.E. Brooks (CNC); ca. 6.5 mi. NE Gasquet nr Cold Spring Mtn, 41°52'15"N 123°53'21"W, 31.v.2009, S.E. Brooks & J.M. Cumming (CNC).
<i>Microphorella</i> Nearctic sp. 6	<b>USA:</b> Oregon: Douglas Co., ca. 7 mi. SW Camas Valley, Bear Crk. Recreation Site, 42°58'08"N 123°45'55"W, 27.v.2009, J.M. Cumming & S.E. Brooks (CNC); Josephine Co., Selma, Squaw Creek, 42°16'47"N 123°38'46"W, 25.v.2009, J.M. Cumming (CNC).
<i>Microphorella</i> Nearctic sp. 10	<b>USA:</b> California: El Dorado Co., South Fork American River, Eagle Rock river access, 38°46'34.6"N 120°16'00.7"W, 18.vii.2012, S.E. Brooks & J.M. Cumming (CNC).
<i>Microphorella</i> Nearctic sp. 13	<b>USA:</b> California: San Mateo Co., Portola Valley, Alpine Road, Corte Madera Creek, 24.vi.1984, 230 m, P.H. Arnaud, Jr (USNM).
<i>Microphorella praecox</i> Loew	<b>Poland:</b> Polish Silesia, Karlowitz, 10.v.1846, H. Loew (ZMHB); Posen, 1.v.1841/14.v.1842, H. Loew (ZMHB). <b>Switzerland:</b> Valais, Leuk-Pfynwald, 27.v.1999/16.v.2000, sweeping above gravel in Rhône River floodplain, B. Merz/H. Ulrich (ZFMK, MHNG, CNC).
<i>Microphorella</i> S. Africa sp.	<b>South Africa:</b> Western Cape: Tradouw Pass, Groot Vaders Bosch, 33°56'52"S 20°42'26"E, 300 m, 30.ix.-22.x.2004, MT in meadow, Irwin, Parker, Hauser (CNC).
<i>Microphorella similis</i> Brooks	<b>Switzerland:</b> Valais, Leuk-Pfynwald, 27.v.1999/16.v.2000, sweeping above gravel in Rhône River floodplain, B. Merz/H. Ulrich (ZFMK, MHNG, CNC).
<i>Microphorella vockerothi</i> Brooks & Cumming	<b>Canada:</b> Nunavut: Kugluktuk 67.78463° -115.279789°, mesic, pan traps, 5-12.vii.2010, NBP field party (LEMQ); Yukon Territory: Dempster Hwy km 135-145, 14.vi.1984, spruce-willow for., car net, S. & J. Peck (CNC).
<i>Neothalassius triton</i> Brooks & Cumming	<b>Chile:</b> Aconcagua, Algarrobo, rocky coast, 23.xi.2006, S.A. Marshall (MNHNS); Coquimbo Region, Punta Teatinos, 13.x.1957/16.ix.1952, G. Kuschel (USNM); Los Lagos Region, Chiloé Island, Chepu, x.1958, on seashore, G. Kuschel (USNM); Valparaiso Region, Cachagua, shoreline rocks, 32°34.90'S 71°27.40'S, 8.xii.2008, Kits & Marshall (UGIC).

.....continued on the next page



TABLE 1. (Continued)

Taxon	Collection Locality
<i>Neothalassius villosus</i> Brooks & Cumming	<b>Chile:</b> Aconcagua, Algarrobo, rocky coast, 23.xi.2006, S.A. Marshall (MNHNS); Tarapacá, Cuya, 26.ix.1957, on sea rocks, G. Kuschel (USNM). <b>Peru:</b> Lima, 15 km W, rocky littoral zone, 19.iii.1975, M.E. Irwin (EMEC, females).
New Caledonia sp.	<b>New Caledonia:</b> South Province: Parc provincial de la Rivière Bleue, R. Bleue nr refuge, 20–21.vii.1995, yellow pans, B.J. Sinclair (CNC).
<i>Parathalassius blasigii</i> Mik	<b>Portugal:</b> Minho, Braga, Esposende, Apúlia, Parque Natural do Litoral Norte, 41°28'24.0"N 08°46'26.6"W, 11.vii.2011, sandy beach, Rui Andrade, (CNC). <b>Tunisia:</b> La Marsa, 8.v.1913 (USNM).
<i>Parathalassius infuscatus</i> Brooks & Cumming	<b>USA:</b> California: Santa Barbara Co., Surf Beach, Vandenberg Air Force Base, 34.683801°N 120.605520°W, 21.iii.2016/5–6.iv.2016/11.ii.2017, sandy coastal foredune, A.J. Abela (CNC); San Luis Obispo Co., Oso Flaco Dunes, 35.032931°N 120.629882°W, 11.ii.2017, A. Abela (CNC).
<i>Parathalassius sinclairi</i> Brooks & Cumming	<b>USA:</b> Washington: Pacific County: Cape Disappointment State Park nr. Ilwaco, Benson Beach, 46°16'20.4"N 124°04'25.4"W, 1–2.vii.2014, swept dunes & beach grass ( <i>Ammophila</i> ) S.E. Brooks, J.M. Cumming & S.H. Cumming (CNC).
<i>Parathalassius wheeleri</i> Brooks & Cumming	<b>USA:</b> California: Humboldt Co., Samoa Dunes Recreation Area, 40°45'41"N 124°13'37"W, 21.v.2009, S.E. Brooks & J.M. Cumming (CNC); Oregon: Lane Co., Suislaw North Jetty, nr. Florence, 44°01'07.0"N 124°08'12.6"W, 7–8.vii.2014, S.E. Brooks & J.M. Cumming (CNC).
<i>Plesiothalassius capensis</i> (Smith)	<b>South Africa:</b> Western Cape: Buffelsbaai, 6.xi.1991, H. Ulrich (CNC); Swartkop, N of Port Elizabeth, 14.x.1982, T. Griswold (LACM); West Coast NP, Duinepos, 33°11.660'S 18°08.305'E, 0 m, 22–23.x.2012, P. Cerretti, J. Stireman, J.E. O'Hara, I. Winkler, A.H. Kirk-Spriggs (CNC).
<i>Plesiothalassius natalensis</i> Ulrich	<b>South Africa:</b> KwaZulu-Natal: Mtunzini, 7.x.1991, H. Ulrich (CNC).
<i>Thalassophorus arnaudi</i> Brooks & Cumming	<b>Canada:</b> British Columbia: Ridley Island, 54°14.13'N 130°19.80'W, 15–17.viii.2008, shore/beach with rocks, logs & boulders, S.E. Brooks & J.M. Cumming (CNC). <b>USA:</b> California: Del Norte Co., Crescent City, Enderts Beach, 41°41'59"N 124°08'31"W, 1.vi.2009, ex. seashore rocks, S.E. Brooks & J.M. Cumming (CNC).
<i>Thalassophorus spinipennis</i> Saigusa	<b>Japan:</b> Hokkaido: Rishiri Island, Oshidomari, Fujino, Pon-moshiri, ca. 45°14'N 141°13'E, 29.v.2008, M. Satô (CNC); Rebun Island, Komaynosaki, Kafukai, 24.vi.2012, M. Satô (CNC).
<b>Dolichopodidae s.str.</b>	
Hydrophorinae	
<i>Paraphrosylus praedator</i> (Wheeler)	<b>Canada:</b> British Columbia: Graham Island, Queen Charlotte City, 9.vii.1960, J.R. Vockeroth (CNC); Ridley Island, 54°14.13'N 130°19.80'W, 15–17.viii.2008, shore/beach with rocks, logs & boulders, S.E. Brooks & J.M. Cumming (CNC). <b>USA:</b> California: Monterey Co., 6 mi. S Lucia, 11.viii.1968, D.D. Monroe (CNC).
Sciapodinae	
<i>Heterosilopus squamifer</i> Hardy	<b>Australia:</b> New South Wales: Kur-ring-gai Chase NP (CNC); Royal NP, Couranga Trail, 7.xi.1993, B.J. Sinclair (CNC).

**TABLE 2.** Character state matrix for Parathalassiinae cladistic analysis (characters 1–79). Outgroup taxa are listed at the beginning of the table. Missing states are indicated by a “?”, inapplicable states are indicated by a “-” and polymorphic states are indicated by a “\*.”.

	1111111111222222222233333333334444444444555555555566666666667777777777
	123456789012345678901234567890123456789012345678901234567890123456789
<i>Anomalempis archon</i>	0000010000000000-00000010000000000000000000210000000000000--000000110000012000101
<i>Apalocnemis</i> Costa Rica sp.	000001000000000001000000000000000000000000000100000001000000--000000000000010000100
<i>Microphor</i> spp.	0000010000000000-100001000000001000001000100000110010000--000000000010020002001
<i>Schistostoma armipes</i>	0000010000000000-1000010000001001000001000100000110010000--000000000010020000001
<i>Plesiothalassius capensis</i>	1000001011101101111011100000000101101110000000011101000100000100001100001112000
<i>Plesiothalassius natalensis</i>	1000001011101101111011100000000101101110000000011101000100000100001100001112000
<i>Amphithalassius latus</i>	1000001111101101111011100000000100101110000000111101000100000100001000001112000
<i>Parathalassius blasigii</i>	1000001111101111111110100010000100101110000000111101001112011102111010021000001
<i>Parathalassius infuscatus</i>	1000001111101111111110100010000100101110000100111101001110111202111110021000001
<i>Parathalassius sinclairi</i>	1000001111101111111110100010000100101110000000111101001112011102111110021000001
<i>Parathalassius wheeleri</i>	1000001111101111111110100010000100101110000000111010011120111021111110021000001
<i>Thalassophorus spinipennis</i>	11000030111011111111111000000002011011*0011100111111001100000110011010021202001
<i>Thalassophorus arnaudi</i>	1100003011101111111111100000000201100110011100111111001100000110011010021202001
<i>Microphorella praecox</i>	1000001111121111111111100011000110101110011100111101001111110102111110001102010
<i>Microphorella similis</i>	1000001111121111111111100011000110101110011100111101001111110102111110001102010
<i>Microphorella curtipes</i>	1000001111101111111111100011000101101110010100111111001110001100111010011000001
<i>Microphorella acroptera</i>	0000001111101111111111100110000101101110010100111101001110101100111011021000001
<i>Microphorella</i> Nearctic sp. 13	0000001111101111111111100110000101101110010100111101001110101100111011021000001
<i>Microphorella chiragra</i>	1000001111101111111111100010000101101110010100011111001110001200111010121000001
<i>Microphorella longitarsis</i>	1000001111101111111111100010000101101110010100011111001110001200111010121000001
<i>Microphorella</i> Nearctic sp. 6	1000001111101111111111100010100101101110010100011111001110001200111010121000001
<i>Microphorella vockerothi</i>	100001001110111111111110001100010110111001111001110100111000111110010021000001
<i>Microphorella chillcotti</i>	100001001110111111111110001100010110111001111001110100111000111110010021000001
<i>Microphorella emiliae</i>	1000003111101111111111100010000100101110011100010121001101001200111010021101001
<i>Microphorella malaysiana</i>	110000111110111111111110000000010111110011100111101101100000100101110021102001
<i>Microphorella iota</i>	1000001111101111111111100000000100101110010100011101001100000100101010021000001
<i>Microphorella</i> Nearctic sp. 2	100000111110111111111110000000010111110010100111101101100000110101000021002000
<i>Microphorella</i> Nearctic sp. 10	100000111110111111111110000000010111110010100111101101100000110101000021002000
<i>Microphorella</i> Chile sp.	1000001111111111111111100010000101101110010100111101001100001100100010021000001
<i>Microphorella</i> Australia sp.	10000011111011111111111000000001001011100101000111011011000001001000??????????
<i>Microphorella</i> S. Africa sp.	0000001111121111111111100000000100101100011100011101001110000100100110021102001
<i>Microphorella merzi</i>	100001201110111101111110000000010011112011100011101201100000200101110021002000
<i>Eothalassius platypalpus</i>	10001120111111111111110000000010011112011100011101201100000200101110021002000
<i>Eothalassius gracilis</i>	10001120111111111111110000000010011111001110001110120110000020010111002?002000
<i>Eothalassius borkenti</i>	100010201111111011111100000001010111110011100011101101100000200101010021002000
New Caledonia sp.	0000011111101011011111100010010100111113111100011101001100000100101010021000001
<i>Chimerothalassius ismayi</i>	0000010011101111011111100000010100111113111100011111001100000100101010021002101
<i>Chimerothalassius runyoni</i>	00000100111011110111111000000101011111311110001111101100000100101010021002101
<i>Neothalassius triton</i>	11100020??101111011111101000010100111113110101111101001100101100101010021000001
<i>Neothalassius villosus</i>	11100020??10111101111110100001010010111311010111111001100101100101010021000001
<i>Paraphrosylus praedator</i>	100110201100110101110110000001120020112011000011120121-0--000100001010021000001
<i>Heterosilopus squamifer</i>	100110201101101-1110100000000120021111001000001020121-0--001100001010021002001